A ZONE-OF-INFLUENCE MODEL TO PREDICT THE EFFECT OF TREES ON THE SPATIAL DISTRIBUTION OF UNDERSTOREY VEGETATION AND SOIL PROPERTIES IN A BOREAL SCOTS PINE STAND

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Summary

A zone-of-influence model was used to predict the effect of approximately 80 years old pine trees on the spatial distribution of understorey vegetation and soil properties in a boreal Scots pine forest. The influence zones around individual trees, expressed as relative influences (0-1), were modelled as rotations of negative-exponential functions, the shape of which depends on tree size. An algorithm was developed to compute the *influence potential*, describing the joint effect of multiple surrounding trees at a specific point in the understorey. Measured ecosystem properties included composition of understorey vegetation, height growth of pine seedlings and top soil characteristics. The relationship between the derived influence potential and measured ecosystem properties was examined using correlation analysis; spatial analyses and comparisons were carried out using semivariogram analysis and spatial interpolation.

The computed influence potential of canopy trees correlated most strongly with species composition of understorey vegetation, humus layer thickness and associated properties, and height growth of pine seedlings so that the growth of seedlings was retarded in the vicinity of trees. All these variables showed a similar overall pattern of spatial variation as the influence potential. The analysis suggests that the arrangement of large canopy trees largely regulates the spatial structure of understorey vegetation, humus properties and height growth of tree seedlings in the understorey in the studied Scots pine forest.

The applied influence potential approach, derived from the ideas of the ecological field theory, provided a useful way to describe the spatial effects of canopy trees on the understorey vegetation and top soil properties in the examined rather poor Scots pine forest. For the development of the method, more attention should be paid to the separate and accurate description of the spatial effects of individual trees on resource levels, and soil and vegetation properties in different forest types.

Introduction

In forests, trees usually play a dominating role in the competitive hierarchy of the plant community and they also have a profound influence on many central ecosystem properties, such as distribution of energy, water and carbon. Accordingly, in their surroundings mature forest trees appear to exert a strong effect on both understorey vegetation (Aaltonen 1919) and soil properties (e.g. Zinke 1962, Boettcher and Kalisz 1990). These effects are obviously due to multiple processes, such as shading, interception of precipitation, foliage and branch litter, root uptake of water and nutrients, root turnover and rhizosphere effects. When considering a stand of trees it is logical to assume that the joint spatial influences of trees should have an effect on the overall spatial distribution of understorey vegetation and soil properties.

This paper reports a study in which a zone-of-influence model, derived from the ecological field theory approach (Wu et al. 1985, Walker et al. 1989), was used to predict the influence of canopy trees on the composition of understorey vegetation and humus soil properties in a boreal Scots pine (Pinus sylvestris L.) stand growing in eastern Finland. The analysis utilizes studies of the same sample plot that have emphasized the different components and aspects of the system, namely humus properties (Hokkanen et al. 1993a), relationships between understorey vegetation and environment (Hokkanen et al. 1993b) and relationships between seedling height growth and environment (Kuuluvainen et al. 1993).

Material and methods

Study area

The study area is located in a Scots pine forest growing in eastern Finland on a rather poor Vaccinium site type (62° 40' N; 29° 45', 105 a.s.l.). The bedrock is composed of sedimentary rocks, the majority being fine-grained mica gneisses. The predominant mineral association in the area is composed of quartz, biotite and plagioclase. The study area is topographically rather even, the difference between the highest and lowest point being about 2 meters.

The canopy trees were about 80 years old. The canopy trees were mapped and measured within a plot that was 180 m in the west-east direction and 150 m long in the south-north direction (2.7 ha). Within this plot a central 100 m by 100 m area was inventoried for seedlings, understorey vegetation, and top soil characteristics. The canopy trees in the buffer zone, 40 m wide in west and east and 25 m wide in south and north, were used in the estimation of canopy tree influences within the one hectare central area (Kuuluvainen et al. 1993).

The inner one hectare area contained 397 canopy trees. The canopy cover in this area was patchy, containing one fairly big opening and several smaller gaps of different sizes (Fig. 1a). Understorey vegetation consisted mainly of dwarf shrubs (Calluna vulgaris, Vaccinium myrtillus, V. vitis-idaea), mosses (Pleurozium schreberi, Hylocomium splendens, Dicranum sp.) and lichens (Cladonia sp.). There were patchy but plentiful naturally regenerated Scots pine seedlings both in gaps and under tree crowns.

Sampling scheme

The inventory of the inner one hectare plot was based on one square meter plots located at 5 m intervals in west-east and south-north directions. Radiation and understorey vegetation was measured at 419 locations, from which a subset of 106 locations was selected for soil sampling. Soil samples were collected in September 1989.

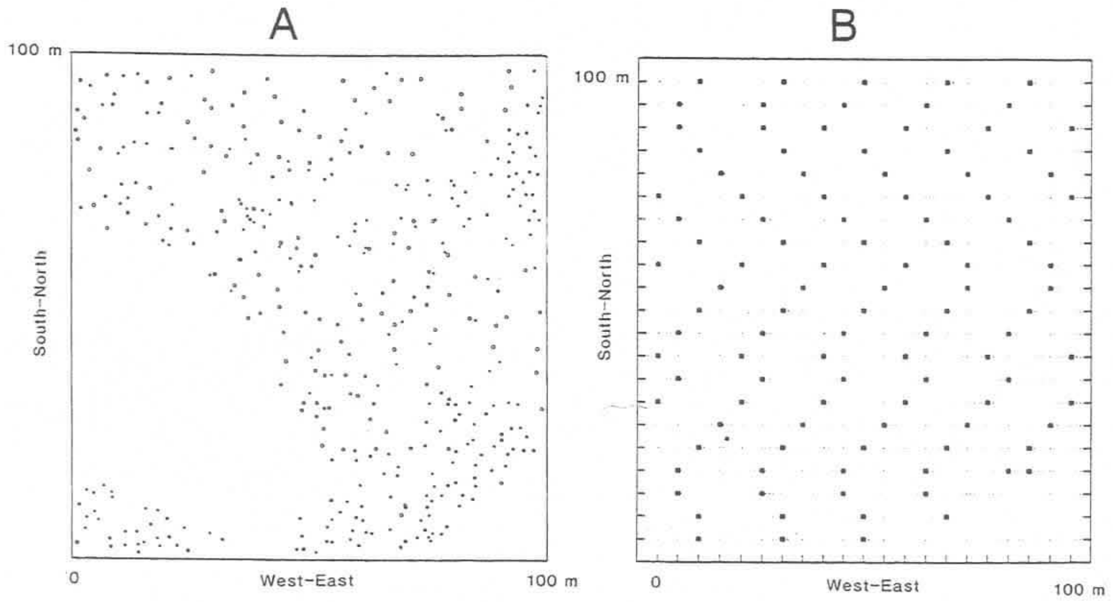

Figure 1. (a) The spatial distribution of trees on the one hectare plot; the size of the circle is proportional to the breast height diameter of a tree. (b) The applied sampling scheme; the crossings of hatched lines indicate locations of radiation and understorey vegetation measurements. The black squares indicate the locations of soil and seedling sampling.

Soil samples from the top 0-5 cm (A_0-horizon and upper stratum in A-horizon) were taken systematically over the area, 20 meters apart along the sampling lines in an east-west direction. At each location, a one square meter plot was sampled using a soil corer, six core samples per plot; the cross sectional area of the corer was 25 cm^2. Live vegetation and litter were removed from each core. All core samples from one square meter plot were combined to form a composite sample for each layer. Top soil was analyzed for pH, electrical conductivity, total N, total C, loss of ignition and soil respiration using standard methods (Hokkanen et al. 1993a).

The momentary irradiance was measured in all 419 locations of the one square meter plots using a Licor PAR sensor. The measurements were taken 3 meters above ground level in order to prevent the tallest seedlings from shading the sensor. Measurements were taken over the one hectare area four times on a clear day in June. Since the diurnal distribution of sun elevations at this time of the year is approximately similar to those of the growing season (Kuuluvainen and Pukkala 1987), the measurements are representative for the season as well. In order to avoid systematic errors due to the movement of the sun, the plot locations were measured every time in a different order. The mean irradiance of the four measurements for each point was used as a relative measure of the radiation conditions at that point.

Description of trees, seedlings and other vegetation

All trees thicker than 5 cm at breast height were measured for coordinates and breast height diameter. The 2.7 ha plot had 1241 trees out of which 123 trees were measured for height, height of crown base and crown diameter. These measurements were used to compute regression equation that gives tree height as a function of breast height diameter (see Pukkala et al. 1993).

Within the one hectare study area, 245 one square meter plots were occupied by at least one seedling. In these plots the three tallest seedlings were measured for total height and height increment of the three past years.

A vegetation inventory was done on 419 one square meter plots. The percent cover of each plant species in the field layer (vascular plants) and in the bottom layer (mosses and lichens) was estimated for each rectangular plot (Hokkanen et al. 1993b).

Description of canopy tree influences

We assumed *a priori* that many of the influences of large trees in their vicinity are approximately symmetrically distributed and distance dependent in such a way that the influence decreases with the distance from the tree (Fig. 2). In this study the concept of influence potential (IPOT) is used to refer to the relative influence of all canopy trees in the 2.7 ha plot at a given point of sampling in the inner one hectare plot (Wu et al. 1985, see also Woods 1984). Influence potential ranges from the maximum of 1 (one) near a big tree to the minimum of 0 (zero) at greater distances (Fig. 2). The effect of one tree on the influence potential was described with one function (Equation 2). This function was taken from the study of Kuuluvainen and Pukkala (1989), which analyzed the effect of Scots pine seed trees on the density on seedlings and understorey vegetation on a similar site with trees of approximately the same age as in the present study.

The combined effect of all trees on influence potential at a given point is computed with the aid of growth potential (GPOT), which is an estimate of the amount of growth resources (Wu et al. 1985, Kuuluvainen and Pukkala 1989). Growth potential at each point of sampling (p) is obtained as a product of the influences of all individual trees (n) on the plot:

$$\mathrm{GPOT}_i(p) = \prod_{i=1}^{n} \llbracket 1-\varnothing_i(s_i(p)) \rrbracket \qquad (1)$$

where

$$\varnothing_i(s) = \varnothing_i(O)\exp(-b_i s^2) \qquad (2)$$

$\varnothing_i(s)$=influence of tree i at distance s (m) from the tree; s=the distance from the tree to the calculation point p; $\varnothing_i(O)$=the effect of tree i at the point of tree location, b_i=parameter. Parameters $\varnothing(O)$ and b depended on tree size as follows: $\varnothing_i(O)=d/35$ and $b=1/(0.4h)$, where d is breast height diameter (cm) and h is the height (m) of the tree (Kuuluvainen and Pukkala 1989).

The influence potential (IPOT) is defined as:

$$\mathrm{IPOT}_i(p) = 1 - \mathrm{GPOT}_i(p) \qquad (3)$$

Seedling height growth

A linear regression between the mean height and the mean height increment of the three tallest seedlings in the one square meter plots was calculated The residual variation around this regression line was related to environmental variables. This measure was preferred because it largely removes the effect of seedling age or developmental stage on the growth variable, since both relative and absolute growth rate of trees are known to change with age or stage of development. In the following discussion this residual variation in mean seedling height growth in the one square meter plots is referred to as seedling height growth and abbreviated as RVSG (Kuuluvainen et al. 1993).

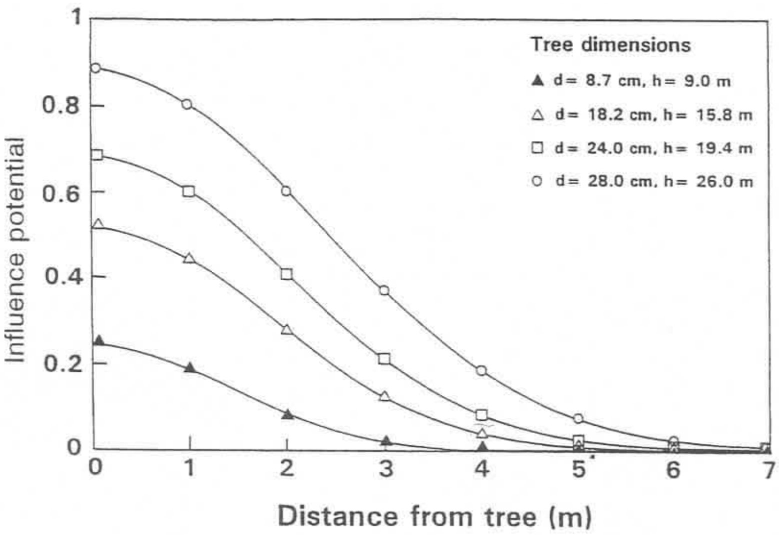

Figure 2. The effect of tree size on the influence of a individual tree as a function of distance trom the tree according to equation (2)

Statistical analyses

Multivariate analyses were used to summarize the variation in understorey vegetation and humus layer characteristics. Factor analysis was used for humus properties (Hokkanen et al. 1993a). Canonical correspondence analysis (CCA) was used to summarize the variation in understorey species composition (Jongman et al. 1987, Hokkanen 1993b). The ordination scores of the first vegetation axis, describing the arrangement of species along the light gradient, were used as the measure of species composition at each location. High score values indicate species associated with high light levels (e.g. Cladonia sp. Calluna vulgaris), while low score values indicate species associated with lower light levels (e.g. Vaccinium myrtillus, Pleurozium schreberi, Hylocomium splendens). (Hokkanen et al. 1993b).

The degree of association between the influence potential and specific variables was assessed using the Spearman rank correlation coefficient (r_s). Nonparametric correlation was chosen because the distributions of the studied variables could not always be normalized. To reduce the degree of autocorrelation among the variables (see Fig. 3), a subsample of 55 plots was taken so that the distance between plots was at least 10 m; in this subsample 30 plots had at least three seedlings. The remaining low or moderate levels of autocorrelation of the variables should not greatly affect the significance tests of the correlation coefficients (Cliff and Ord 1981: 189).

The analysis of spatial variability and autocorrelation was carried out using variogram analysis (e.g. Legendre and Fortin 1989) and bivariate spatial interpolation (SAS/GRAPH 1988). The computer programs presented by Robertson (1987) were used to calculate semivariances. For the spatial pattern analysis of the different understorey plant species and soil properties, we used the spatial interpolation technique available in the G3GRID default procedure of the SAS/GRAPH (1988: 479-488). This method interpolates values from an irregularly spaced set of points, calculating a rectangular grid of interpolated values. The method consists of first dividing the the sample site into triangles using Delaunay triangulation and then fitting a bivariate fifth degree polynomial within each triangle. For computational details see SAS/GRAPH (1988). Because of the patchy distribution of understorey vegetation and because the sample points are evenly distributed across the study area, this method displays well the spatial variation in the measured variables (SAS/GRAPH 1988).

Results and discussion

Association between influence potential and measured variables

The correlation between the influence potential, and understorey vegetation and humus properties was first examined using the score values, derived from multivariate analyses, summarizing the variation in these ecosystem components. The influence potential correlated significantly with the CCA vegetation axis 1 score values ($r_s=0.36$, $p<0.01$, $n=55$), which describe the arrangement of species along the light gradient (Kuuluvainen et al. 1993). This relationship suggests that species like Vaccinium myrtillus and feather mosses thrive close to the trees, while species like Calluna vulgaris and Cladonia sp. are more associated with openings.

The influence potential correlated weakly significantly with the humus factor 1 scores ($r_s=0.33$, $p<0.05$, $n=55$), describing humus layer thickness and associated properties (Hokkanen et al. 1993a). This means that the thickness of the organic humus layer decreased with increasing distance from the adjacent trees. This pattern can be attributed to processes like greater litter accumulation under the trees accompanied by lower decomposion rates due to interception of precipitation by trees crowns. Especially, low moisture content can apparently strongly inhibit humus decomposition on dry sandy sites. The observed litter accumulation in the vicinity of the trees may also be partly attributed to lower soil temperatures, due to both lower radiation receipt and the insulating humus layer. Accordingly, decrease in influence potential was related to increased decomposition and proportion of nitrogen in organic matter (Hokkanen et al. 1993a).

The influence potential also correlated significantly with seedling height growth (RVSG) ($r_s=-0.50$, $p<0.01$, $n=30$) (Kuuluvainen et al. 1993). This indicates that the joint distance dependent influences of canopy trees strongly influence the height growth of understorey pine seedlings, so that the height growth is retarded in the vicinity of trees. It is evident that large trees affect seedling growth both directly (e.g. through resource competition) and indirectly via their strong effect on the properties of understorey vegetation and humus layer (Kuuluvainen et al. 1993).

The question to what degree the influence potential reflects the shading effect is difficult to answer, because the different above- and belowground tree influences overlap in space. However, since the influence potential around individual trees was assumed to be symmetrical while shading due to interception of beam radiation is not (Kuuluvainen and Pukkala 1987, Pukkala et al. 1993), the spatial distributions of influence potential and shading are only partly overlapping in space. This also shown by the only moderate correlation between the influence potential and radiation ($r_s=0.43$, $p<0.001$, $n=55$). In addition, the fact that the seedling height growth (RVSG) did not correlate with measured radiation ($r_s=0.12$) would indicate that the derived influence potential reflects mainly tree influences other than shading. Especially belowground influences and root competition apparently play a significant role in regulating understorey seedling growth in poor Scots pine forests (Aaltonen 1919, Björkman and Lundeberg 1971).

Spatial analysis

The omnidirectional variograms showed that the variances of CCA vegetation axis 1, humus factor 1, seedling height growth (RVSG) and influence potential of canopy trees all increased in a similar manner across the range of distances examined (Fig. 3). This fact together with the correlations mentioned above suggest that the effects of large trees, as described with the computed influence potential, largely regulate the spatial structure of understorey vegetation and humus properties in the examined pine forest. The semivariograms, however, exhibit considerable variation and nugget effects, which may indicate short scale variability not detected by the present sampling sheme.

A spatial interpolation technique revealing small-scale spatial variation was further used to analyze the relationship between influence potential and the abundance distribution of specific understorey species (Fig. 4). The two most abundant dwarf shrubs, Calluna vulgaris and Vaccinium myrtillus, had different responses to the tree influence potential. Calluna vulgaris was most abundant in the south-west corner of the area, where the biggest gap is situated, but it was also present in patches under the more dense canopy (Fig. 4b). In contrast, Vaccinium myrtillus was absent in the large opening, but was found in patches of different size in the northern end of the plot, where the influence potential is in general highest (Fig. 4c). A common lichen, Cladonia rangiferina, showed a third type of response, by being most abundant in the northern end of the large gap, where both Calluna vulgaris and Vaccinium myrtillus were less abundant (Fig. 4d). Cladonia rangiferina was also abundant near tree trunks where dwarf shrub competition was minimal (Hokkanen et al. 1993b). It is possible that the distribution of lichens in the bottom layer is largely regulated by the spatial distribution of dwarf shrubs. In general, Figures 4b-d show the patchy nature of distribution of these understorey species, which is at least partly due to their clonal growth habit.

The height increment of seedlings was most rapid in and around the large gap, but also responses to smaller gaps in the forest can be detected by comparing Figs. 4a and 4e. This indicates that the influences of trees, as determined by their size and arrangement, largely regulates the spatial pattern of the height growth of understorey seedlings and, evidently, their recruitment into the main canopy.

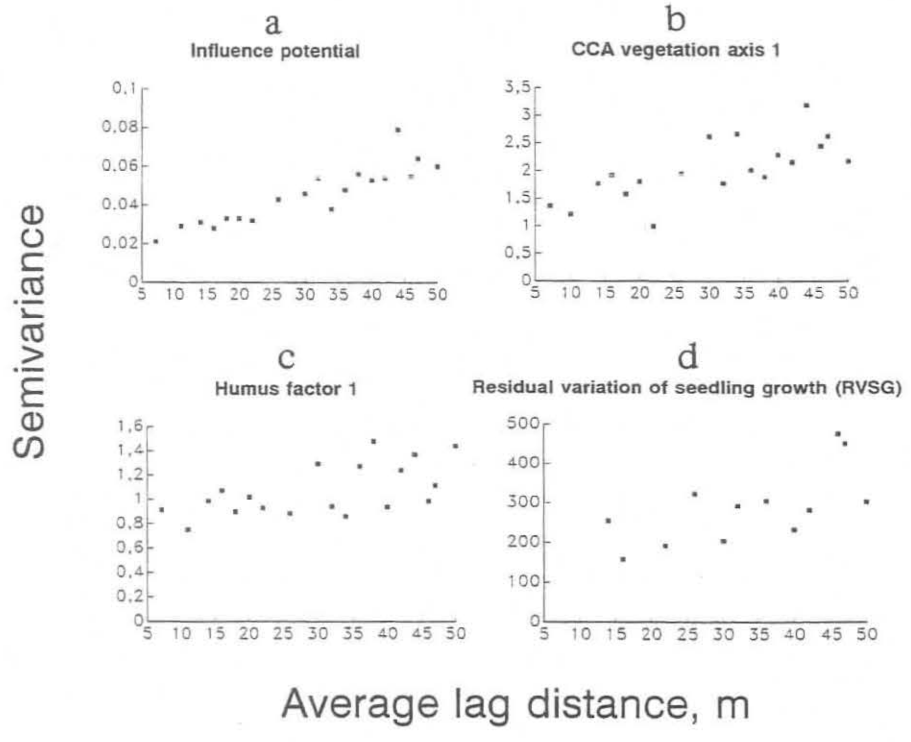

Figure 3. Omnidirectional semivariograms for (a) the computed influence potential of canopy trees, (b) the first axis of the canonical correspondence analysis (CCA vegetation axis 1), describing the arrangement of understorey species along the light gradient, (b) humus factor 1, indicating humus thickness and associated variables and (c) residual variation of mean seedling height growth.

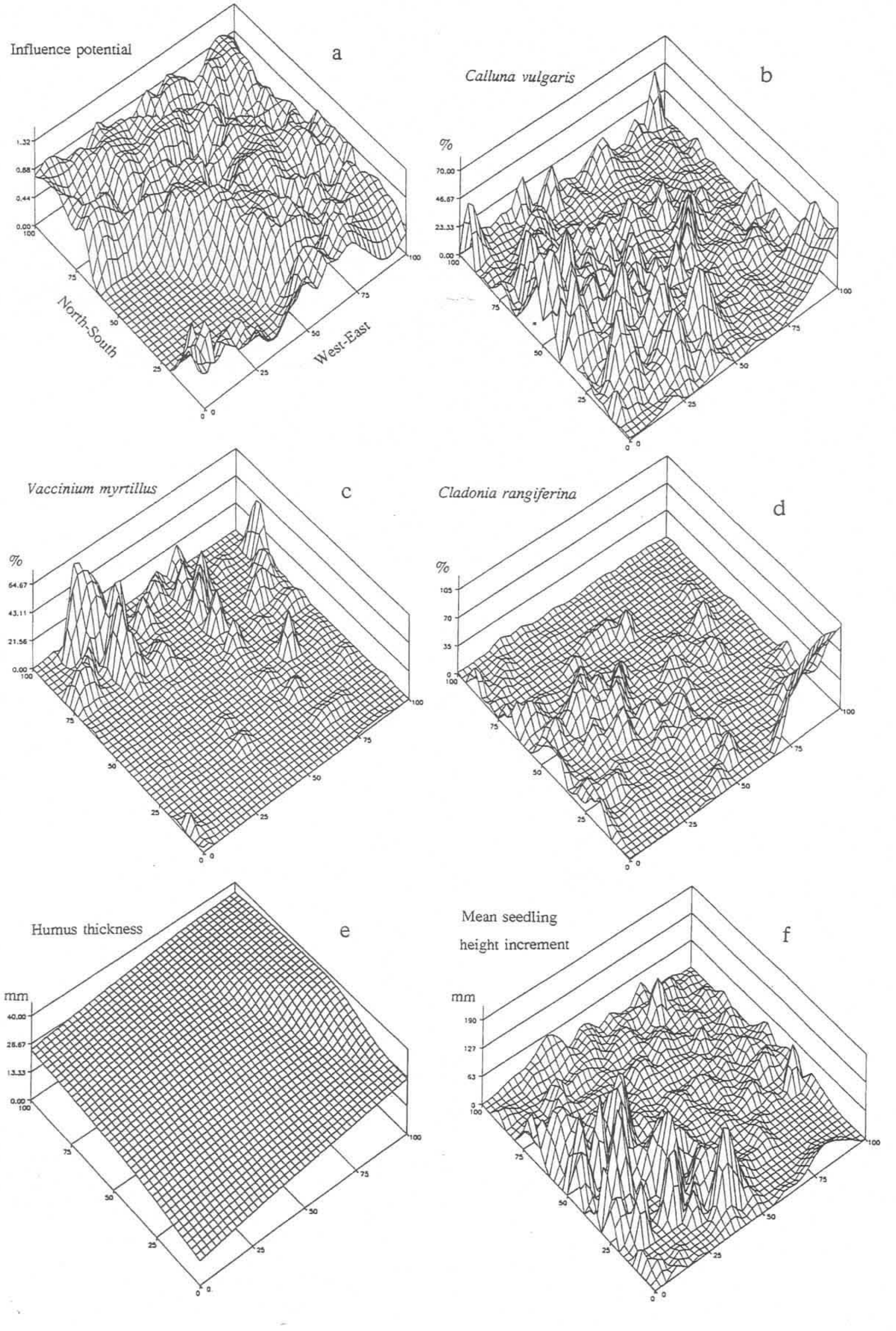

Figure 4. Spatial distributions of influence potential (a), cover percentages of Calluna vulgaris (b), Vaccinium myrtillus (c), Cladonia rangiferina (d), humus thickness (e) and seedling height growth (f) as obtained by spatial interpolation. For vegetation the number of measured points was 419 and for humus thickness 106.

Conclusions

A zone-of-influence model was used to predict the spatial effects of large trees on the understorey components of a boreal Scots pine forest. The applied zone of influence model was found useful in predicting the effects of Scots pine trees on the understorey vegetation, top soil properties and seedling height growth. The results indicate that in the studied Scots pine forest large canopy trees largely regulate the spatial pattern of understorey plant species composition, humus properties and seedling recruitment. Accordigly, this modelling approach could be useful in predicting the effect of forest structure on understorey plant species composition and diversity, and pattern of natural regeneration. Furthermore, the described approach to model the competitive interference between canopy trees and small seedlings could be used in spatially explicit gap models to more realistically describe the effect of gap structure on the pattern of seedling growth. It is possible, however, that the applicability of this approach is limited to forests growing on poor and/or dry sites where belowground interferences dominate over light competition, the spatial variation of which is inherently more difficult to predict (Pukkala et al. 1993). For the development of the method, more attention should be paid to the separate and accurate description of the spatial effects of individual trees on the levels of different growth factors, and soil and vegetation properties in different forest types. The assumption of directional uniformity of tree influences should be examined, and possibly elaborated in order to account for nonsymmetrical effects like shading.

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